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## **The competitive edge: competition and biofilm composition, an individual-based modelling approach**

B. J. R. Cockx\*, R. J. Clegg\*\*, S. Lang\*\*\*, J. Kreft\*\*, B. F. Smets\*

\*Department of Environmental Engineering, Technical University of Denmark, Bygningstorvet 115, 2800 Kgs. Lyngby, Denmark (E-mail: [baco@env.dtu.dk](mailto:baco@env.dtu.dk))

\*\*Centre for Computational Biology, Institute of Microbiology and Infection, School of Biosciences; University of Birmingham, Edgbaston, Birmingham B12 5TT, United Kingdom

\*\*\*Department of Bioinformatics, Friedrich Schiller University, Ernst-Abbe-Platz 2, 07743 Jena, Germany

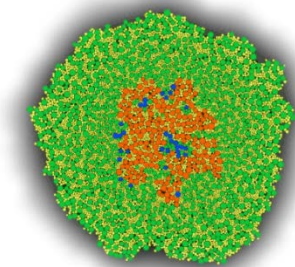
Mixed culture biofilms can consist out of countless microbial species or strains all with their own traits and features. Many of these traits may be regulated by a network of genetic switches responding to environmental cues, resulting in a biofilm with a diversity of phylotypes and phenotypes. Even though environmental conditions can impose strong selective pressures, in an open system, the microbial community compositions can shift substantially and can be unpredictable due to other internal and external effects (Ju, 2015). Drift may partly contribute to this unpredictability of community composition, as by interplay of stochastic processes new species may be introduced to the biofilm while others disappear. This drift by itself may result in shifting cooperative or competitive interactions resulting in a further community shift.

Reliable predictions on community composition can typically only be made on the presence of obvious traits such as metabolism based on available chemical species and increased resistance to local environmental conditions such as pH, temperature or the presence of environmental compounds. Because of the complexity of typical microbial communities it can be difficult if not impossible to study the competitive effects of more nuanced differences in traits in the context of the community experimentally. Individual based microbial community models provide a platform to study the effects of these traits individually. We apply the new individual based modelling platform iDynoMiCS 2 to study the effects of individual traits on microbial community composition and structure.

In the context of the recent discovery of Comammox Nitrospira, a group of Nitrospira that may perform complete ammonium oxidation, we study the occurrence of AOB and NOB (division of labour) dominant and communities with high Comammox Nitrospira abundance. Currently there are no published studies of kinetic parameterisation of Comammox Nitrospira and there is no strict consensus on AOB and NOB kinetics either (Shielke-Jenni, 2015). Yet even with a not fully characterized microbial community, a modelling approach can clarify in what scenarios complete ammonium oxidation can be beneficial over division of labour. As the aim of this study is not to parameterise the microbial community, but to gain an understanding of what conditions favour the split labour strategy over the full ammonium oxidation strategy. Our kinetic model extends on previously published modelling studies (Pérez, 2009), extending it with an estimated parameter set for Comammox Nitrospira. Here we focus on the relative differences amongst microbial species that determine their competitiveness rather than characterising them for one specific system.

We evaluate the hypothesis by Costa et al. (2006) that for growth in clonal clusters (such as in a biofilm) Comammox species have an advantage over split metabolic labour nitrification by achieving a greater growth yield. By exploring a collective of scenarios we study whether this hypothesis holds in an individual-based model and under which conditions. Furthermore we evaluate whether there may be other aspects that promote complete ammonium oxidizing over the split metabolic labour strategy.

Spatial distribution and structure of the microbial groups within a microbial aggregate is commonly observed, and can explain effects in community composition (Picioreanu, 2016). Here we focus on two typical structures commonly found in microbial aggregates: stratification and the formation of micro-colonies. Stratification is commonly recognized as the result of environmental gradients (such as substrate, inhibitor or pH gradients). We hypothesize that in a stratified biofilm the spatial positioning in terms of relative distance from the biofilm surface(s) is a direct result of substrate affinity and resistance to environmental factors of the combined community. As a result the introduction of a microbial species (or mutation) that shifts the kinetic properties of one microbial guild can cause a ripple effect that changes the relative abundance of all other microbial groups.



**Figure 1:** Stratification in a partial nitrification anammox granular biofilm model implementation. The model was developed with the iDynaMiCS framework. Agents are represented as spherical particles in the model. The model includes anammox (orange), nitrite oxidizing bacteria (blue), ammonium oxidizing bacteria (green) and extracellular polymeric substances (yellow).

Like stratification, the formation of micro-colonies may also impact community composition. A recent modelling study by Picioreanu et al. (2016) demonstrates that smaller micro-colonies may provide a competitive advantage due to improved substrate availability. We hypothesize that the formation micro-colony is driven by the same effects as aggregation. This may include sharing of common goods, lack of motility and thus dispersion and to some extent also the protection against outside environmental factors. We are interested in what processes may govern micro-colony formation, size and distribution within a biofilm. We pose that only two mechanisms may result in the formation of a micro-colony; either by the attachment of a planktonic bacteria or micro-aggregates to an existing biofilm, or by the splitting of micro-colonies that are already embedded within the biofilm. Due to the restrictive movement within a biofilm, we would expect clustering of micro-colonies formed by colony splitting, opposed to more randomly distributed micro-colonies due to attachment from outside the biofilm.

We hypothesize that a higher rate of attachment would result in a more yet smaller micro-colonies due to increased substrate competition amongst the colonies. When concerning colony splitting the attachment strength between sibling cells (filial attachment) is likely governing the size and amount of micro-colonies, as it is more likely a micro-colony splits up when there is no specific attachment

formed with sibling cells (neutral attachment) in comparison to a strong filial attachment scenario. Extending on this we study whether subtle differences in attachment properties may indirectly shift the composition of the microbial community by regulating micro-colony size.

Rather than focussing on effects imposed by the environment, we attempt to unveil the effects on microbial community composition that result from subtle differences in the properties of the embedded organisms.

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